THE USTILAGINEÆ, OR SMUTS; WITH A LIST OF ILLINOIS SPECIES.

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These plant parasites are popularly known as "smuts," of which the sooty bunches, several inches in diameter, found on the stalks and ears of maize are familiar and conspicuous examples. While the mycelium in a large number of the species is indefinitely scattered throughout the tissues of the infected plants, the spores are usually formed in or sometimes on definite organs of the host — most commonly of the flower or fruit. The primary infection often arises from the penetration of the germ tube into the succulent parts of very young seedlings. Once gaining entrance the mycelium grows with the development of the infected tissues, and so perhaps spreads throughout the whole plant, early reaching the young ovary or other spore-forming region, where it extensively develops, often causing much distortion and final destruction of the affected organ.

There is therefore in most annual plants but one generation per year, but in some perennials the mycelium lives from year to year. The spores have, more or less pronounced, a period of rest after maturity, often germinating most readily in autumn or spring when the plantletts of the proper host normally appear. But some leaf-dwelling kinds, *e. g.*, species of Entyloma, are less specialized as to season of the year, germinating freely at maturity, even before distribution from the producing plant.

Some species of Entyloma and Tubercinia produce coni-

dia as well as the usual spores of other kinds of Ustilagineæ. These conidia are colorless, simple cells, borne singly on the tips of special branches of the mycelium, which push from beneath through the epidermis in more or less densely aggregated clusters or patches. They are thin-walled, rounded, or much elongated, and when considered by themselves are classed in such genera as Ramularia, Cylindrospora, etc. As they are ephemeral, germinating at once and soon losing this power, they appear to be for the temporary but rapid distribution of the parasites. The germ tube immediately penetrates the epidermis of the host, or first forms at its apex by constriction a sporidium from which the germ tube proper is emitted. Such ephemeral spores are common in other families of fungi, but are exceptional productions in the Ustilagineæ.

Returning now to the development of the lasting spores, or those common to all the species, it is to be said that considerable difference exists as to the method of production among the species constituting the group. Most often the fertile portions of the mycelium are densely aggregated within limited areas in the host, and the spores are produced in such numbers — each being a minute, dark-colored sphere — that the mass becomes black and powdery. With the species of Tilletia the spores are typically formed within the terminal parts of short, lateral mycelium branches, one in each, while with those of Ustilago the richly-branched, specialized, spore-forming threads, interlaced and compacted, produce in irregular rows the numerous spores throughout their length. In this genus the fertile threads become gelatinized and swell to several times their first diameter, and at the same time little shining globules of protoplasm collecting within the filaments develop into spores, having at length fully formed walls inside the contour of the enlarged thread. Gradually the latter softens, and at last disappears, leaving the powdery mass almost wholly composed of spores. In the

case of Entyloma the fertile hyphæ are not so strongly differentiated from the mycelium, are less compacted, and the spores do not form a powdery mass. Here the spores are either formed at the apex of a branch, as in Tilletia, or along the course of a filament, as in Ustilago.

In these now named, with others, the ripe spores are free from each other; but in some genera they are more or less firmly coherent — twin in Geminella and Schizonella and from few to many in others. Each spore is, however, physiologically separate, and however united in special groups are equal among each other except in the genus Urocystis. In this case the definitely formed balls have one spore or a few larger central spores, possessing the power of germination, surrounded by sterile, spore-like bodies. It is difficult to make out the process of spore-development within the dense clusters, but the ball-like collection arises from the branches of one or more mycelium-filaments closely coiled and intertwined. The spores are formed within the knot while the sterile filaments surround them upon every side.

The germination of the spores has been much studied within recent years. While there is found much of similarity and uniformity in the process for the whole group, there are certain differences that are supposed to be the best foundations for generic distinctions. It now seems doubtful, however, if the genera at present recognized can be rigidly separated into really natural groups even with this important aid. The development is quite different in pure water from that in a nutrient solution, as Brefeld* has beautifully shown. Then again it is by no means certain that the observed phenomena in artificial cultures are such as occur in the natural germination of the spores upon the host plants, a thing very difficult to make out.

In nearly all cases a slender tube is first sent forth through a rupture of the outer coat of the spore. This tube

* Botanische Untersuchungen über Hefenpilze. 1883.

is called the promycelium. In ultimate size, mode of branching, and sporidia-production it varies considerably in the different species, and upon these differences the generic distinctions are largely based. The typical form in Ustilago is a slender, unbranched tube, divided by cross partitions into cells, from each of which elliptical or oval sporidia are produced as lateral outgrowths. In nutrient solutions these last mostly assume yeast-like forms and manner of growth. Brefeld, however, shows that certain species are quite exceptional in their germinative processes, as follows:

(1). Sporidia never yeast-like; lateral branches like the promycelium, — *Ust. longissima, grandis, bromivora.*

(2). No promycelium; sporida direct from spore, becoming yeast-like in nutrient solutions, — *Ust. olivacea.*

(3). Sporidia in liquids few and scarcely yeast-form, usually elongating into threads which upon reaching the air form terminal conidia similar to the spores of certain moulds, — *Ust. destruens.*

(4). True sporidia rarely formed; the promycelium becoming a long, slender, septate, branched thread whose joints often separate in artificial cultures and continue independent growth, —*Ust. Crameri, Rabenhorstiana, hypodytes, neglecta.*

The promycelium and sporidia of the species of Tolysporium are similar to the type form in Ustilago. Quite another type is found in the species of Tilletia, Entyloma, Melanotænium, Tubercinia and Urocystis. Here the promycelium is short, continuous or septate, unbranched, with a whirl or crown of elongated sporidia at its apex. The caphora is related in germinative characteristics to the third exceptional form named above for Ustilago, and Sorosporium to the fourth form. In case of Schrœteria, the spherical sporidia are formed at the end of the simple promycelium, by constriction, in a single row, differing in this respect from all other Ustilagineæ.

A peculiar fusion of the sporidia, sometimes while still attached to the promycelium, often takes place. Not unfrequently the same phenomenon is observed between the adjoining cells of the promycelium itself, and sometimes between the promycelia of different spores. This union takes place at the point of accidental contact or in many cases by the outgrowth of lateral protuberances from each of two sporidia lying parallel with each other in such manner that an H-like figure is produced. The apices of the two lateral growths meet, fusion takes place, and the two sporidia with their connecting tube becomes one cell. The uniting tubes may arise from either end as well as from the middle of the sporidia, but always reach out directly towards each other. In other cases the sporidia themselves regularly curve so as to meet two and two at their ends and directly fuse into one. Or when lateral branches instead of sporidia proper are produced (*e. g.*, Thecaphora) one from above a septum of the promycelium bends downward, while another from below bends upward, thus meeting and fusing. Union rarely occurs between three or more sporidia, and never, it seems, as a regular procedure.

For the most part in the further germinative development all agree in the production of a single tube from the united pair, and into this tube the entire protoplasm of the whole passes. This, however, is not different from the germination of impaired sporidia except perhaps in the vigor of growth. With or without fusion secondary sporidia are often produced from those of the first order instead of the young mycelium just mentioned. These secondary sporidia bud out from the first ones just as the latter spring from the promycelium, taking, in the same way, the entire protoplasm of the older part. The secondary sporidia again give rise under some circumstances to a generation of the third order, and these perhaps to a fourth. The germ tube that penetrates the host plant and becomes a new mycelium may therefore come

directly from the promycelium itself, from branches of this, or from primary, secondary, etc., sporidia, and apparently in any case with or without pairwise fusion. It ought however to be said that the union by pairs in numerous species appears to be the normal method of development, for example with *Tilletia caries*, *Ustilago segetum*, *Tubercinia trientalis*, while with many others it is apparently accidental.

It is an open question whether or not this union is sexual in significance. DeBary * takes the affirmative, Brefeld † the negative view. Probably in these low plants sexual difference is not decidedly attained, yet is sufficiently marked to be of some importance. In this respect a distinction can be made between sexuality and bi-sexuality. Certainly there can be little of the latter in the Ustilagineæ; but there is no reason why we may not suppose the observed phenomena indicate the existence of the former, and that the unions are truly sexual in character. This does not forbid equal development without the conjugating process, for the sexual distinction must be slight at best. We must think of it as somewhat favorable, but not strikingly beneficial, certainly not essential. With this view, it cannot be decisively objected that the union takes place at an irregular or improper stage in the life history of the plant, though it may serve to show that the Ustilagineæ are not closely related to those groups in which an imperative conjugation or fertilization precedes the formation of the lasting spore. There is nothing to show that the Ustilagineæ are degraded from forms once possessing this latter peculiarity of development.

A question remains as to the systematic position of the Ustilagineæ as a group among other plants. Their homologies are by no means certainly ascertained. Authorities hold decidedly diverse views upon the true relationships.

Most commonly the plants are associated with the Ure-

* Morphologie und Biologie der Pilze, pp. 155–188.

† Botanische Untersuchungen über Hefenpilze, p. 172, etc.

dineæ and are by some held to be closely allied to them. The two groups have been united under the name Hypodermii,* and as DeBary temporarily accepted this association, the name itself with the implied relationship of the plants has often been ascribed to him. But as early as 1853 he † discusses the characteristics of the two groups and advances reasons for keeping them separate. Bessey ‡ places the two groups near together with the idea that they should be considered aberrent forms of Ascomycetes. In this he finds confirmation in the development of the spores of Ustilago, etc., *within* a fertile branch of the mycelium, and in the similarity of some telentospores (Phragmidium) to asci.

Brefeld § puts the Ustilagineæ into the class Oomycetes, which is made to include the following orders: (1) Chytridiaceæ, (2) Saprolegineæ, (3) Peronosporeæ, (4) Entomophthoreæ, (5) Ustilagineæ. He argues that the last two are connected through Entyloma and that the ball-forming species of Urocystis are represented by Mortierella among the Zygomycetes. DeBary, in his recent work, *Morphologie und Biologie der Pilze* [1884] pp. 198–199, endeavors to show that the Ustilagineæ are related through Protomyces and Cladochytrium to the Chytridieae. In this case forms classed under Entyloma must stand next the Protomyces as the lower types of the group from which two diverging series may be recognized, reaching on one hand the ball-forming kinds like Sorosporium and Urocystis, and on the other those with well-defined and well-developed fruit-bodies like *Ustilago* (*Sphacelotheca*) *hydropiperis*.

From all that can be gathered from the literature of the subject and from a study of the plants themselves, it seems probable that the group, though standing quite decidedly by

* Fries. Systema Mycologicum III [1829], p. 504.

† Untersuchungen ueber die Brandpilze, pp. 98–100.

‡ Botany for High Schools and Colleges, pp. 310–320.

§ Botanische Untersuchungen ueber Schimmelpilze, IV [1881], pp. 162–165.

itself, and so distinct from all others, still approaches those kinds having undoubted sexual organs and known methods of conjugation or fertilization. Without admitting the degeneracy assumed by some from these latter, it may rather be supposed that they were divided off before these higher characteristics became fixed as they are now found. Very possibly the Chytridieæ may represent the earliest forms from which the Saprolegneæ, Entomophthoreæ, Peronosporeæ, and Ustilagineæ have sprung by development in diverging lines. When more is known of the significance of the fusion of the sporidia of the other parts of the germinative apparatus, clearer indications may be found upon this subject of systematic position and relation. At present we cannot form a positive conclusion.

The Ustilagineæ include many species that are seriously destructive to cultivated crops. All the plant diseases known as smuts are due to them, or rather the fungi themselves are the smuts. From ten to fifteen per cent. of the products of fields of wheat, oats, and maize is often destroyed, and fifty or even still higher per cent. of loss has been known, through the blighting influences of the species affecting these important crops. In certain regions of the country this is much more liable to occur than in others, without any well-known cause for the difference. In the great wheat-growing district of the Pacific slope, as well as throughout some of the Atlantic States, bunt, or stinking smut (*Tilletia caries*), is vastly more injurious than in the wheat fields of the Mississippi valley. Onion smut (*Urocystis cepulæ*) is especially bad in Connecticut. In Illinois and elsewhere *Ustilago segetum* is much more common on oats than upon wheat, but in some instances the reverse is true.

The only method of prevention proved to be reliable is washing the seed (as of wheat) with pure water or with solutions like copper sulphate. The benefit derived in this way is believed due either to killing the spores or separating them

from the seed with which the latter are infected from the smutted grain of the preceding year. In some instances, however, even this process seems to have little or no effect, as with the smut of onions and of maize. In such cases it is supposed the spores exist for months in a living condition in the soil, ready to germinate and penetrate the young host plants when the latter commence their growth.

Though some of the smuts are conspicuous enough, the species are mostly obscure productions, and sharp as well as trained eyes are necessary for their collection. As microscopic objects little claim can be laid to beauty, though the singular sculpturing of some spores make them worthy of attention in this respect. For certain tests the spores even of the smut of corn may scarcely be surpassed. But the main interest to the microscopist must be in the systematic study of the species, and especially in the careful following of development, — the life histories of the minute plants. The internal mycelium can best be examined by boiling for a few minutes the tissue containing it in a strong aqueous solution of caustic potash, then separating the parts by gently pressing upon the cover glass, or by grinding the softened material under the cover, using by preference a rubber-tipped pencil for this purpose. Sometimes the mycelium can be beautifully demonstrated in thin sections of the infected host by staining in an aqueous solution of eosin for some hours, then decolorizing to the proper degree in common alcohol. In successful attempts the fungus will be stained a conspicuous red color, while the tissues of the host are unstained. But this process does not succeed with all specimens, neither is there any method known by which the desired result can be certainly attained. The difficulty, of course, is to stain the fungus without staining the elements of the host plant. No doubt the method of decolorizing to the required amount will always be found most serviceable.

The technical description of the family may be as follows:

Fungi parasitic in the tissues of the vascular plants. Mycelium internal, usually widely scattered between the cells of the host, consisting of delicate, colorless, septate branched filaments, in many cases sending haustoria into the cells as curled, bushy-branched appendages; spores commonly of but one kind, produced within or upon the host from specialized portions of the mycelium, either at the end of fertile branches or intercally along the filaments, one-celled, free or two to many united in ball-like clusters, at maturity generally becoming a black, powdery mass, and producing on germination a delicate, colorless promycelium, which for the most part bears colorless, sessile, sporidia from which (with or without previous fusion, two and two) may arise the final germ-tube that penetrates the plant tissues and becomes a new mycelium.

GENERA OF USTILAGINEÆ.

Ustilago, — Spores when ripe free from each other, forming a powdery mass, produced in irregular rows or groups, within specialized, bushy-branched, closely aggregated hyphæ putting forth a septate promycelium from each joint, of which one or more sporidia are borne as lateral outgrowths.

Tilletia, — Spores when ripe free from each other, forming a powdery mass, produced singly within the swollen end of short branches of aggregated fertile hyphæ, upon germination producing a short, usually septate, promycelium which bears at its apex a whirl of fusiform or filiform sporidia which commonly conjugate two and two and then, from the united pair, send forth a sporidium of the second order.

Entyloma, — Spores single, not forming at maturity a dusty mass, produced singly in the apex, or here and there in the course of the loosely aggregated fertile hyphæ, sending forth on germination a promycelium bearing two to several elongate sporidia at its apex, which with or without conju-

gation give rise to delicate germ tubes, or to sporidia of a second order.

Melanotænium, — Spores free from each other, formed singly in the course of the fertile hyphæ, producing in germination a septate promycelium which bears a whirl of branch-like sporidia that often conjugate.

Doassansia, — Spores at maturity free from each other, pale or without color, produced in isolated sori surrounded by a special membrane composed of a single layer of pallisade-like cells, sending forth in germination a short, simple promycelium, bearing a whirl of apical, elongate, conjugating sporidia.

Testicularia, — Spores at maturity free from each other, produced as a peripheral layer in granules which form powdery masses in numerous cavities of a well-defined stroma. Germination unknown.

Cintractia, — Spores at maturity free from each other, produced in a peripheral, compact mass from a central stroma, germinal tubes simple, not (so far as known) bearing sporidia.

Graphiola, — Spores at maturity free from each other, produced in a beaker-shaped, orumpent peridium, sending forth in germination a simple, nonseptate promycelium, which bears singly but in succession non-conjugating sporidia. On palms.

Urocystis, — Spores united and, with somewhat similar sterile exterior cells, forming ball-like clusters, which are produced from two or more spirally twined or irregularly clustered hyphæ, which, together with a covering of matted filaments, form a compact knot with the true spores in the center; in germination producing a short promycelium which bears an apical whirl of sporidia that seldom conjugate.

Sorosporium, — Spores united in firm, ball-like clusters of equal units, produced (in *S. saponaria*) from closely associated, many-jointed, interlaced, and consolidated filaments;

each spore sending forth in germination a simple septate promycelium without sporidia.

Tubercinia, — Spores united in fine, ball-like clusters of many equal units, arising (in *T. trientalis*) from closely associated, many jointed, interlaced, and consolidated filaments, each spore sending forth a simple promycelium bearing a whirl of sporidia upon its apex.

Tolysporium, — Spores equal, closely associated in spheroidal clusters, in germination producing a septate, unbranched promycelium, which bears lateral, conjugating sporidia.

Thecaphora, — Spores equal, united in coherent clusters, producing in germination an elongate, septate promycelium from each joint of which proceeds a lateral branch that conjugates with a neighboring branch of the same promycelium.

Schizonella, — Spores joined in pairs by a small isthmus or connecting part, formed by division of a single cell, producing in germination a short, septate promycelium with lateral non-conjugating sporidia.

Schrœteria, — Spores joined in pairs with broad, contact surfaces, formed from spirally wound, special branches of the mycelium; in germination producing a short promycelium bearing several sporidia, either in an apical whirl (?), or in a terminal, chain-like row.

LIST OF SPECIES COLLECTED IN ILLINOIS.

USTILAGO.

U. Austro-Americana, Speg.	On Polygonum incarnatum.
U. hydropiperis (Schum.), Winter,	On Polygonum acre.
U. neglecta, Niessl.	On Selaria glauca.
U. Rabenhorstiana, Kühn,	On Panicum sanguinale.
	On Panicum glabrum.
U. segetum (Bull), Ditm.	On wheat and oats.
U. sorghi (Link), Winter,	On broom-corn and sorghum.
U. spermophorus, B. & C.	On Eragrostis poæiodes.
U. sphærogena, Burrill,	On Panicum crus-galli.
U. syntherismæ, Schno.	On Panicum prolifereum.
	On Cenchrus tribuloides.
U. utriculosa (Nees), Tul.	On Polygonum incarnatum.
U. zeæ-mays (D C), Winter,	On maize.

TILLETIA.

T. caries (D C), Tul.	On wheat.
T. striæformis (West.), Niessl.	On Phleum pratense.

ENTYLOMA.

E. compositarum, Farlow,	On Eupatorium ageratoides.
	On Ambrosia trifida.
	On Ambrosia artemisiafolia.
E. linariæ, Schrt.	On Veronica peregrina.
E. menisperme, Farl. and Trel.	On Menispermum Canadense.
E. microsporum (Ung.), D By.	On Ranunculus repens.

CINTRACTIA.

C. junci (Scluo.), Trelease,	On Juncus tenuis.

SOROSPORIUM.

S. Ellisii, Winter,	On Andropogon scoparius.

UROCYSTIS.

U. anemones (Pers.), Winter,	On Hepatica triloba.
U. occulta (Wallr.), Rabh.	On unknown grass.